LETTER

Sport science for salmon and other species: ecological consequences of metabolic power constraints

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Abstract

For metabolically demanding behaviours, power supply (ATP resynthesis per unit time) is an important constraint on performance. Yet ecology as a discipline lacks a framework to account for these power constraints. We developed such a framework (borrowing concepts from sports science) and applied it to the upriver migration of anadromous fish. Our models demonstrate how metabolic power constraints alters optimal migratory behaviour; in response to strong counter flows, fish minimise cost of transport by alternating between rapid, anaerobically fuelled swimming and holding to restore spent fuels. Models ignoring power constraints underestimated the effect of elevated water temperature on migration speed and costs (by up to 60%). These differences were primarily due to a temperature-mediated reduction in aerobic scope that impairs the ability of fish to rapidly migrate through warm waters. Our framework provides a mechanistic link between temperature-induced reductions in aerobic scope and their ecological consequences for individuals, populations and communities.

Keywords

Aerobic, aerobic scope, anaerobic, critical power, endurance, metabolic power constraints, migration, recovery, river, salmon.

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INTRODUCTION

One common theme among the diversity of behaviours organisms use to survive and reproduce is that they all are fuelled by energy. Although the physiological and behavioural mechanisms involved in converting chemical energy to performance (the execution of a metabolic or mechanical action, e.g. somatic growth, swimming) are complex, ecologists have a long and successful history of abstracting these complexities down to simple mathematical representations, and using these representations to evaluate optimal behaviour and its consequences in variety of ecological contexts.

Yet predictions of optimal behaviour will not be accurate unless relevant constraints on metabolic performance are considered (Oudman *et al.* 2014). For energetically demanding behaviours (e.g. strenuous migrations, prey capture, predator avoidance), metabolic power supply (ATP resynthesis per unit time) is an important constraint on performance. In animals, metabolic power demand (ATP use per unit time) for low to intermediate levels of activity is supplied primarily through oxidative phosphorylation. For high-intensity performance, the resynthesis of ATP from oxidative metabolism alone cannot match demand, and the limited ATP stores that animals have on hand are sufficient to cover this deficit for just a few seconds. However, performance can be prolonged through the synthesis of ATP from glycolysis and phosphocreatine (PCr) breakdown, which, because they do not require oxygen, are often referred to as anaerobic metabolism. Eventually, cellular

energy stores of glycogen and PCr are depleted, the demand for ATP exceeds supply, performance drops, and the complex process of recovery begins (Gleeson 1996). The physiological mechanisms that underpin exhaustion and recovery and their implications for ecological and evolutionary processes continue to be an active area of research (Pörtner & Knust 2007; Clarke & Pörtner 2010; Vanhooydonck *et al.* 2014). Yet unlike the equally complex processes involved in whole-organism energy dynamics, ecologists have not yet abstracted the complexity involved in metabolic power supply to simple mathematical form. Because of this, ecology as a discipline lacks a general framework for incorporating the effects of power constraints on optimal behaviour and evaluating their ecological consequences.

Metabolic power constraints have received considerable attention from sports science, a discipline that aims to understand the physiological mechanisms that constrain athletic performance and exploit these findings to inform predictive models of human endurance and recovery. One of these models, the Critical Power model, has been used extensively to model performance of metabolically demanding activities (Monod & Scherrer 1965; see Morton 2006; Jones *et al.* 2010 for reviews). The Critical Power model differentiates two sources of power that mirror aerobic and anaerobic supplies. The aerobic source can provide power indefinitely, but only up to a maximum rate or 'critical power', P_c. Demand for power exceeding P_c is supplied from the anaerobic source, N, that is not rate limited, but has finite capacity, referred to as

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the 'anaerobic work capacity', N_{max}. Thus, for any activity with a total power demand, P_t, greater than the critical power, the time until exhaustion, t_e, is:

$$t_e = N_{max}/(P_t - P_c), \qquad (1)$$

and activities with $P_t \leq P_c$, can be performed indefinitely. The model has been extended to include recovery processes, where anaerobic work capacity is treated as a state variable and is depleted or resupplied at a rate proportional to the difference between P_t and P_c (Morton & Billat 2004). This adaptation of the model is especially relevant for behavioural ecology where the consequences of recovery processes (in terms of lost time and energy) must be considered.

When linked with phenomenological or biomechanical models relating power to performance, the Critical Power model can be used to identify optimal power output or pacing strategies for a given activity (e.g. running, cycling; Billat *et al.* 2009; Sundström *et al.* 2014). Although the function to be optimised in ecology and sports typically differs (e.g. cost minimising vs. time minimising) the metabolic processes that constrain them are the same.

Here, we apply the metabolic power concepts from sports science to the swimming behaviour of fish to understand how constraints on aerobic and anaerobic power supply affect predictions for optimal performance in fish migrations. Many anadromous fish species face a metabolically challenging task of swimming vast distances against strong river currents without feeding, where the power requirements for optimal swimming often exceed their maximum aerobic capacities (Ellis 1966; Bernatchez & Dodson 1985). As a result, power constraints should have important consequences for migratory behaviour. Additionally, because fish are ectothermic, water temperature also impacts migratory performance by altering power available for swimming. We developed models to investigate how power constraints affect optimal behaviour of Chinook salmon (*Oncorhynchus tshawytscha*) over a range of river flow and temperature conditions. We then linked our bioenergetics models with a 1-dimensional hydrodynamics model of the Sacramento River in California's Central Valley to predict the consequences of power limitation on whole river migration speed and energetic costs. Finally, we compared the migration speeds predicted by the models to observed migration speeds of Chinook in the Sacramento River. Although we focussed on anadromous fish migrations, the approach demonstrated here is applicable to a broad set of ecological contexts where fitness depends on metabolically demanding performance.

METHODS

We developed and evaluated three models that predict cost of transport (*COT*, energy per unit distance) of migrating fish as a function of their swim velocity U_s, river temperature, T, and river flow velocity, U_c (the water velocity fish must swim against). Model 1 was based on a well-tested energetic model of fish swimming within the aerobic range (Webb 1998; Hein & Keirsted 2011). Model 2 extended Model 1 by linking the swim costs model with the Critical Power model. Model 3 further extended Model 2 by considering the overhead costs of

Table 1 Parameter estimates for the three models (see Appendix S1 for details of parameter estimation)

Symbol	Description	Value	Units
c_0	Intercept for mass-specific maintenance rate (1 kg, 0 °C)	65.51	mgO$_2$ h^{-1} kg^{-1}
b	Mass exponent for mass-specific maintenance rate	−0.217	–
d	Temperature exponent for maintenance rate	0.068	–
c_1	Intercept for swimming cost scalar (1 kg)	420.6	mgO$_2$ h^{-1} kg^{-1} m$^{-\gamma}$
β	Mass exponent for mass-specific swim costs	−0.369	–
γ	Velocity exponent for mass-specific swim costs	2.130	–
P_c	Critical Power	633	mgO$_2$ h^{-1} kg^{-1}
N_{max}	Anaerobic work capacity	103	mgO$_2$ kg^{-1}
y_r	Recovery yield	1.82	–

anaerobic fuel recovery in more detail. For all three models, we calculated the swim speed that minimised *COT* over a range of river temperatures and flow velocities. Using these values, we then compared the three models' predictions for optimal migratory behaviour and its energetic consequences. All powers and *COT* are expressed in mass-specific units (kg^{-1}) (Table 1).

Model 1 (no constraints on power)

The total power requirement, P_t, of a swimming fish is the sum of the power requirements of maintenance metabolism, P_m and of swimming, P_s:

$$P_t = P_m + P_s. \qquad (2)$$

Maintenance rate is assumed to depend on mass, M and temperature, T:

$$P_m = c_0 M^b e^{dT} \qquad (3)$$

where c_0, b and d are empirically derived parameters. We chose the exponential form for temperature dependence rather than the more mechanistic Boltzmann or Arrheinius relationship; over the range of temperatures considered, the two forms are in practice indistinguishable (Hein & Keirsted 2011). We assumed the power requirements of swimming to depend on mass, M and swimming speed U_s:

$$P_s = c_1 M^\beta U_s^\gamma \qquad (4)$$

where c_1, β and γ are parameters. We divided total power, P_t, by ground speed (swim speed–flow velocity) to get the *COT*:

$$COT = (P_m + P_s)/(U_s - U_c). \qquad (5; \text{'Model 1'})$$

This standard model, predicts a 'U-shaped' relationship between *COT* and swim speed (see Fig. S1), where *COT* is minimised at an intermediate swim speed that balances high maintenance costs per unit distance at low speeds against high swim costs per unit distance at high speeds (Webb 1998).

Model 2 (constraints on power supply)

To incorporate power constraints, we assume that swimming at speeds with power demands exceeding P_c must be accompanied by time spent recovering anaerobic fuels. Combining the swim costs model in eqn 5, with the Critical Power model in eqn 1, yields time to exhaustion for a given swim speed and temperature:

$$t_e = N_{max}/(P_m + P_s - P_c). \qquad (6)$$

We assume that fish can make use of readily accessible low flow microhabitat for recovery, for example, that occurs around boulders or debris (Liao 2007). Thus during recovery, fish pay no swimming costs and divert only enough power to pay maintenance costs from recovery. Thus, recovery time, t_r, is:

$$t_r = N_{max}/(P_c - P_m) \qquad (7)$$

Because the time to deplete and restore N are both proportional to N_{max}, the ratio of time spent recovering to time spent swimming is independent of N_{max}, and for the same reason, the proportion of time spent recovering is independent of whether anaerobic fuels are fully or only partially depleted and recovered in a given burst-recover cycle. With the recovery ratio known, we can account for the recovery costs (maintenance costs paid during recovery) associated with swimming at a given speed to the *COT*:

$$COT = \frac{P_m + P_s + P_m \max\left(0, \frac{P_m + P_s - P_c}{P_c - P_m}\right)}{U_s - U_c}. \qquad (8; \text{'Model 2'})$$

Model 3 (constraints on power supply + overhead costs of recovery)

Model 2 assumes the energy required to restore anaerobic work capacity is equivalent to the energy generated by its depletion. However, if recovering anaerobic fuels requires additional energy expenditure, for example to reverse highly exergonic reactions, Model 2 may significantly underestimate *COT*. The anaerobic recovery yield, y_r, defined as the energy required to restore one unit of N, is the weighted average of the recovery yields of all three anaerobic fuels:

$$y_r = \Sigma f_i y_i = f_{ATP} y_{ATP} + f_{PCr} y_{PCr} + f_{Gly} y_{Gly} \qquad (9)$$

where f_{ATP}, f_{PCr} and f_{Gly} are the fraction of anaerobic work fuelled by ATP, PCr and glycogen, respectively, and y_{ATP}, y_{PCr} and y_{Gly} are their recovery yields ($y_i = 1$ when there are no recovery overheads for fuel i). For ATP and PCr, assuming a recovery yield of 1 is reasonable as ATP resynthesis during recovery follows the same biochemical pathway that generates ATP during steady state metabolism (oxidative metabolism), and the restoration of ATP in turn drives the reversible phosphorylation of creatine (Tiidus *et al.* 2012).

Glycogen, the most substantial energy store of the three fuels, can have significant recovery costs. Glycolysis of one muscle glycogen molecule results in two lactate molecules and a net yield of three ATP (Atkinson 1977). During recovery, lactate generated from anaerobic exercise is either used as a substrate for resynthesising glycogen or it is oxidised. Resynthesising glycogen from lactate directly resupplies depleted glycogen stores, but comes at a cost of seven ATP for every three ATP originally generated (Atkinson 1977). Alternatively, converting lactate to pyruvate and using it as a substrate for aerobic metabolism, achieves the same energy yield per unit glycogen as aerobic respiration. On the surface, the strong preference of fish to use lactate as a substrate for gluconeogenesis (Gleeson 1996) appears energetically disadvantageous. However, for animals with no dietary carbohydrate intake (e.g. most adult salmonids do not feed once they start their river migration), oxidation of lactate results in a net loss of glycogen, which must then be synthesised from protein sources. Proteins must be first broken down to amino acids and deaminised before use as a substrate for glycogen synthesis. For most glycogenic amino acids, deamination is an energetically neutral process (Bender 2012). After deamination most glycogenic amino acids follow the same biochemical pathway as lactate for glycogen resynthesis. Thus, for non-feeding animals, oxidising lactate provides no energetic advantage, because the glycogen deficit incurred from oxidising lactate must be recouped using amino acids as a substrate for glycogen resynthesis, which have the same energetic penalty as lactate (seven ATP to recover the three ATP gained from glycolysis). For animals with significant dietary carbohydrate intake, y_{Gly} will significantly lower, as glycogen deficits incurred from lactate oxidation can be replenished from food (Gleeson 1996).

With the recovery yields for all three fuels known, y_r can be calculated by weighting the proportion of anaerobic work generated by each fuel type (see parameterisation section). Incorporating recovery overheads ($y_r > 1$) to Model 2 yields:

$$COT =$$
$$\frac{P_m + P_s + P_m \max\left[0, \frac{y_r(P_m + P_s - P_c)}{P_c - P_m}\right] + \max[0, (y_r - 1)(P_m + P_s - P_c)]}{U_s - U_c}$$
$$(10; \text{'Model 3'})$$

Parameterisation

To estimate the swim cost parameters in eqns 3 and 4, we compiled published respiration datasets on swimming Chinook salmon, and estimated parameters using non-linear regression (details in Appendix S1). In sports science literature, parameters of the Critical Power model are estimated by measuring time to exhaustion at multiple levels of constant power demand. For animals, time-to-exhaustion experiments are generally only conducted at one speed (Endurance tests e.g. Garland 1984), or at incrementally increasing speed ('Critical swim speed' tests for fish; Plaut 2001). These tests alone are insufficient to specify both P_c and N_{max}. Fortunately, the maximum rate of oxygen consumption, VO_{2Max}, a commonly measured trait in ecology, evolution and comparative physiology, can be used to estimate P_c. We assumed P_c is temperature-independent. Although mitochondrial function is temperature dependent, for many aquatic species maximum aerobic rate plateaus at intermediate temperatures, potentially due to capacity-limited ventilation and circulation (Pörtner 2001). Thus, in practice P_c is roughly constant for a broad temperature range (e.g. less than 15% increase in VO_{2Max} of

Chinook between 8 and 12.5 °C, and no increase in VO_{2Max} from 12.5 to 17.5 °C; Geist *et al.* 2003).

For our application, performance is independent of N_{max}. However, it may be needed for other applications and can be estimated from a single time-to-exhaustion experiment if P_c is known (Appendix S1).

We estimated f_i for the three fuels from datasets where the concentrations of each were measured before and after exhaustive exercise. From these data sets we estimated f_i of 0.616, 0.312 and 0.072 for glycogen, PCr and ATP, respectively, resulting in a y_r of 1.82 (see Appendix S1 for details). Although the limited data available for ectothermic animals suggests that glycogen resynthesis is the largest contributor to recovery yield (Hancock & Gleeson 2008), other factors may contribute to y_r (e.g. lactate-induced acid-base regulation, increased futile cycling, and elevated ventilation and circulation rates). Alternatively, increased reliance on PCr over glycogen, could potentially reduce the overhead costs of recovery. To understand how uncertainty regarding the costs of recovery affects predictions for migration performance, we ran simulations assuming overhead costs of recovery were either 25% higher or lower than the nominal value.

Optimal swimming in response to flow velocity and temperature

We compared the predictions of all three models for optimal migration behaviour in response to a range of flow velocities and temperatures. Specifically, we compared model predictions for optimal swim speed, U_s, the proportion of time spent recovering, $t_r/(t_e + t_r)$, or swimming, $t_e/(t_e + t_r)$, migration speed, $[t_e/(t_e + t_r)](U_s - U_c)$, and COT.

Whole river migration costs

The Sacramento River in California supports four runs of migrating Chinook salmon. The majority of the spawning adults will migrate over 500 km from the ocean to near the base of Keswick Dam, where further passage is then blocked. To understand the impacts of power constraints on the speed and energy costs of river migration, we link the three energetic models with physically based hydrodynamic models that estimate water velocity and temperature.

We used HEC-RAS (US Corps of Engineers) to model 1-dimensional hydrodynamics, and RAFT (Pike *et al.* 2013) to model water temperature dynamics. We used model outputs (temperature and velocity) for each 1 km river section at sub-hourly intervals, spanning the years 2009–2013. The model domain covers 390 km of river, starting at the I Street Bridge in the city of Sacramento and ending at Keswick Dam (south of Shasta Dam). We excluded the 80 km lower river section from the San Francisco Bay to the city of Sacramento due to tidal influences that were not adequately captured with the hydrodynamic models.

We ran a suite of simulations to estimate total migration duration and energetic costs. In each simulation, the model salmon had the same weight, 5 kg, but the starting date of migration over the course of the 4-year period varied. At each 1-km interval, we used the flow, velocity and temperature to calculate the optimal swim speed that we in turn used to calculate the energy and time needed to traverse that section. We then summed these values to compute a total time and energy needed to traverse the entire river. We also evaluated the consequences of migration costs on fecundity by assuming Chinook begin their migration with an energy density of 8 MJ kg^{-1}. After spawning, Pacific salmon die with an energy density of approximately 4 MJ kg^{-1}, likely reflecting a minimum threshold for survival (Crossin *et al.* 2004). Thus, we assumed this energy is unavailable for allocation and the remaining 4 MJ kg^{-1} is used to first pay migration costs, and the remainder allocated to reproduction.

Lastly, we compared predicted migration speeds to observed migration speeds of nine acoustic tagged fall-run Chinook salmon that travelled the length of the Sacramento River during the late summer and fall of 2012. They represented the subset of tagged salmon that successfully migrated to the spawning grounds of the Sacramento River. We surgically implanted Vemco V16-4H (VEMCO, Bedford, Nova Scotia, Canada) acoustic tags into the peritoneal cavity of the fish and tracked them using an array of tag detection monitors spread throughout the Sacramento River. We initiated simulations on the dates where each fish was first observed within the model domain. Due to substantial differences in river geomorphology between the lower 175 km (deep, homogenous, and highly leveed) and upper 215 km (un-leveed, heterogeneous, run-riffle river), we separately compared the ability of the models to predict migration speeds (the rate of upstream movement along the one-dimensional channel) in the two river sections.

RESULTS

Optimal swimming behaviour in response to flow

At low flow velocities, the power demands for optimal swimming are lower than P_c, thus all models predict identical migratory performance regardless of whether power constraints were included (Fig. 1). At higher flow velocities, the optimal swim speed of fish without power constraints continues to increase, but in Models 2 and 3, eventually power demand exceeds the critical power ($P_m + P_s > P_c$), and predictions of these models deviate from Model 1. In both models incorporating power constraints, the predicted behavioural response of fish to intermediate flow velocities is to cap swimming speed so that power demand does not exceed P_c. Initially, it is energetically more efficient for power-constrained fish to swim at a slower speed relative to the optimal unconstrained speed, which for a power-constrained fish would require the use of anaerobic fuels. This is because anaerobic fuel recovery in both models incurs an extra cost: maintenance during recovery in Model 2, and additionally the overhead of anaerobic fuel recovery in Model 3. As flow velocity is further increased, the costs of not increasing swim speed outweigh the costs of recovery and the optimal behaviour of fish is to alternate between swimming at unsustainably fast speeds (fuelled in part by depleting N) and resting to recover N. As flow velocity is increased further, the optimal swim speed continues to increase and fish spend an increasing proportion of their time recovering, ultimately slowing their rate of migration.
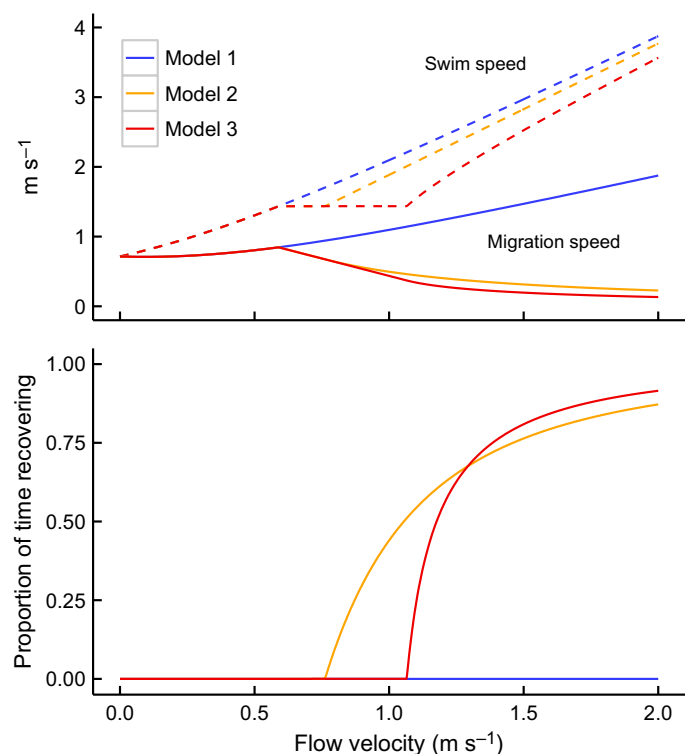
Figure 1 Top panel: Optimal swim speed (dashed lines) and migration speed (solid lines) as a function of the river velocity the salmon must swim against for the three models at 15 °C. Model 1 does not include power constraints, Model 2 includes power constraints, and Model 3 includes power constraints and overhead costs of anaerobic fuel recovery. The bottom panel shows the fraction of time spent recovering $t_r/(t_e + t_r)$ associated with swimming behaviour of the three models in the top panel.

Optimal swimming behaviour in response to temperature

In the absence of power constraints (Model 1), fish minimise COT by swimming more rapidly through warmer waters (Fig. 2). This strategy allows fish to mitigate the costs of travelling through warm, energetically expensive waters by spending less time in them. Furthermore, because migration speed increases with flow velocity, the effect of temperature on COT is actually smaller at high flow velocities, as the fish pay maintenance costs for a shorter duration.

For the two models with power constraints, the relationship between migration speed and temperature is complex. As before, optimal swimming against a slow flowing river does not require the use of anaerobic fuels, thus the effect of temperature on migration speed and costs are identical to the unconstrained model. At high flow velocities, however, temperature switches from speeding up migration to slowing it down. This 'flip' marks the transition to flow velocities where optimal swimming is constrained by power supply. Fish can now no longer escape warm waters simply by swimming more rapidly, because they would also have to spend a larger fraction of their time resting. At higher temperatures, an increasing proportion of available power must be diverted to meet the demands of maintenance metabolism thereby reducing aerobic power available to fuel swimming (i.e. a reduction in aerobic scope, defined as the difference between maximum

and maintenance power; $P_c - P_m$). Thus, for swim speeds requiring power above P_c, fish in warmer waters power a larger fraction of their swimming anaerobically, and consequently exhaust more rapidly (decreased t_e). Furthermore, because anaerobic fuel recovery is powered aerobically, temperature-induced reductions in aerobic scope also slow recovery (increased t_r). Thus, at high flow velocities, temperature slows migration speeds by increasing the proportion of time spent recovering. Lastly, the flow velocity at which power constraints begin to impact optimal swimming decreases with temperature, which is also due to a reduction in aerobic scope.

For all models, COT is more expensive in warm waters. However, warm waters are substantially more costly for power-constrained fish. Due to a temperature-induced reduction in aerobic scope, the migration speeds of power-constrained fish are slower in warm waters. Consequently, in warm waters, power constrained fish pay maintenance costs for a longer period of time, which is further exacerbated because in warm waters maintenance costs are more expensive. Incorporating the overhead costs of anaerobic fuel recovery (Model 3) further magnifies the effects of flow velocity and temperature observed in Model 2.

Consequences for full river migration

Incorporating metabolic power constraints substantially alters model predictions for the duration of the adult migration in the Sacramento River. Without constraints on power, the average predicted migration duration is approximately 4 days; the inclusion of power constraints more than doubles the average migration duration (Fig. 3, top panel), and overhead costs for anaerobic fuel recovery increase migration duration an additional 2 to 5 days. Furthermore, power constraints alter the seasonal pattern of migration duration. As expected from the patterns in Fig. 3, migration duration increases in response to temperature and flow velocity, while the non-constrained model shows the opposite pattern.

For migration costs, the primary difference between models with and without power constraints is the relative contribution of temperature (Fig. 3). As a result, the effects of power constraints and overhead costs of anaerobic fuel recovery on migration costs tend to be greatest in summer to early fall, when the Sacramento River is both warm and relatively fast. Higher migration costs in the power-constrained models result in substantially different estimates of energy allocation to reproduction, especially in periods coinciding with warm river temperatures (Fig. 3).

Comparison to telemetry data

The models incorporating power constraints (Models 2 and 3) always outperform the model without power constraints (Model 1) in predicting observed migration speeds (Fig. 4). In the lower, channelised river section of the river, the mean and distribution of migration speeds predicted by Models 2 and 3 closely match observed migration speeds, while the slowest migration speeds predicted by Model 1 exceed the fastest observed migration speeds (Fig. 4b). In the upper, non-
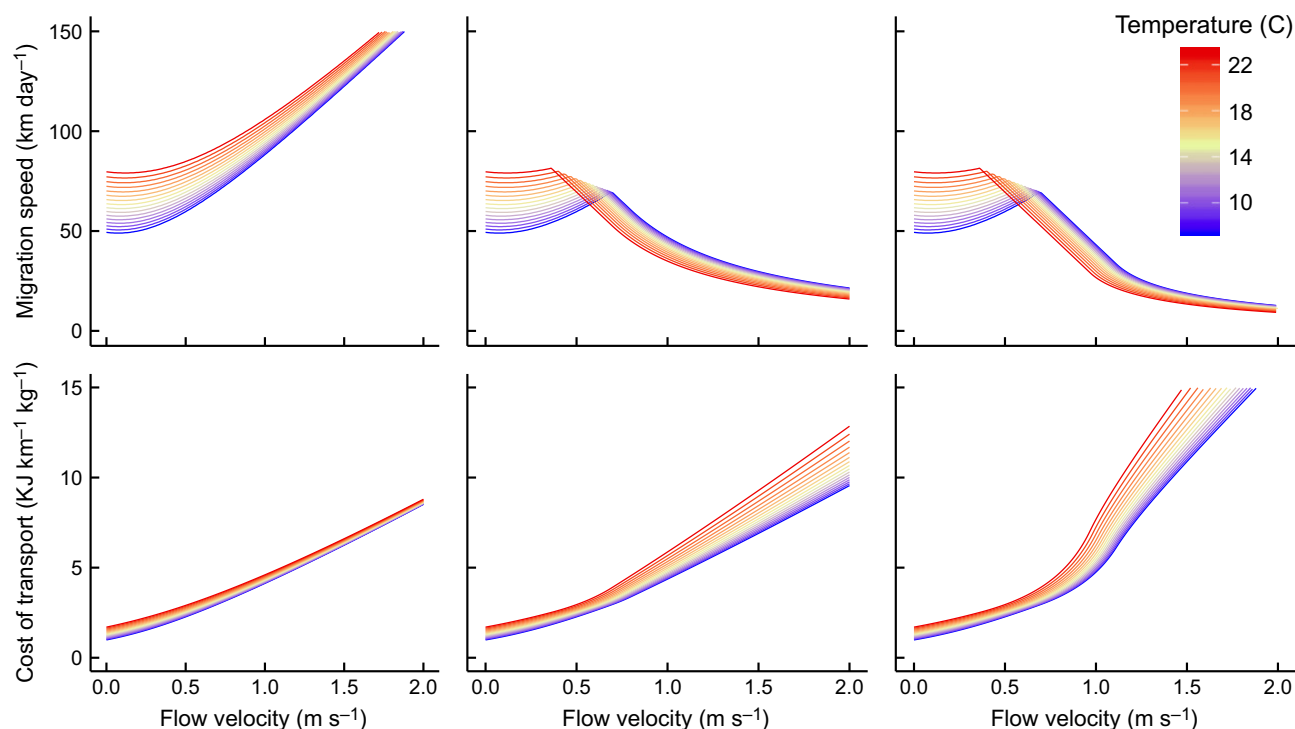
Figure 2 Optimal migration speeds (top panels) and energy costs (bottom panels) of swimming as a function of temperature and flow velocity in Model 1 (no power constraints; left panels), Model 2 (with power constraints; middle panels), and Model 3 (with power constraint and overhead costs of anaerobic fuel recovery; right panels). Predictions are based on a 5 kg Chinook.

DISCUSSION

The recent rise in global ocean and river temperatures along with evidence of temperature-induced mortality during migration (Rand *et al.* 2006) has renewed interest in the link between temperature, aerobic scope and migratory performance for salmon (Farrell *et al.* 2008; Eliason *et al.* 2011). These studies use aerobic scope, as measured from laboratory experiments, to predict the migratory success of salmon. However, because the exact relationship between aerobic scope and migratory performance is context-dependent and not known *a priori*, the relationship must be determined statistically for each context. The approach developed here resolves this problem by directly linking aerobic scope and migratory performance. More broadly, it provides a generic framework for linking temperature-induced reductions in aerobic scope and their consequences in a wide range of ecological contexts.

Standard models of swimming energetics, which do not incorporate metabolic power constraints, substantially underestimate the effect of temperature on migration costs (Fig. 2). In the absence of metabolic power constraints, fish could mitigate the costs of warm waters by swimming through them

channelised river section, all models overestimated migration speeds, but the mean migration speeds predicted by Models 2 and 3, deviate less from observations than Model 1. In the upper river sections, observed fish that arrived earlier show a strong tendency to hold for long periods between monitor locations (Fig. 4a).

quickly. As a consequence, *COT* was largely insensitive to temperature in Model 1. Constraints on power supply impair the ability of fish to migrate through warm water, through a reduction in aerobic scope, resulting in longer migration times that are especially costly due to temperature dependent maintenance costs. Our results may still underestimate the true costs of increased temperatures, as we assumed that aerobic scope was reduced only by increased power demand for maintenance, while experiments with sockeye salmon populations have demonstrated at very high temperatures, aerobic scope is further reduced by a collapse in aerobic power supply (Eliason *et al.* 2011). However, when data are available to characterise power supply (P_c) as a function of temperature for a species it can easily be incorporated to the models presented here.

The consequences of a reduction in aerobic-scope depend on the power demands of optimal swimming; hot, fast moving rivers are especially costly. Under natural conditions, this combination might rarely impact Pacific salmon migrations; periods of high river discharge are associated with cooler water from winter rains or from spring snowmelt. However, in highly regulated rivers where dams alter the natural hydrography, the seasonal relationships between temperature and flow are often substantially altered from natural patterns. In the Sacramento River, discharge is unnaturally high in the summer to meet agricultural demands. This period of warm, fast rivers overlaps with migration timing of the majority of Fall-run Sacramento Chinook, the largest run in the state, in the late-summer through early fall (Williams 2006). During
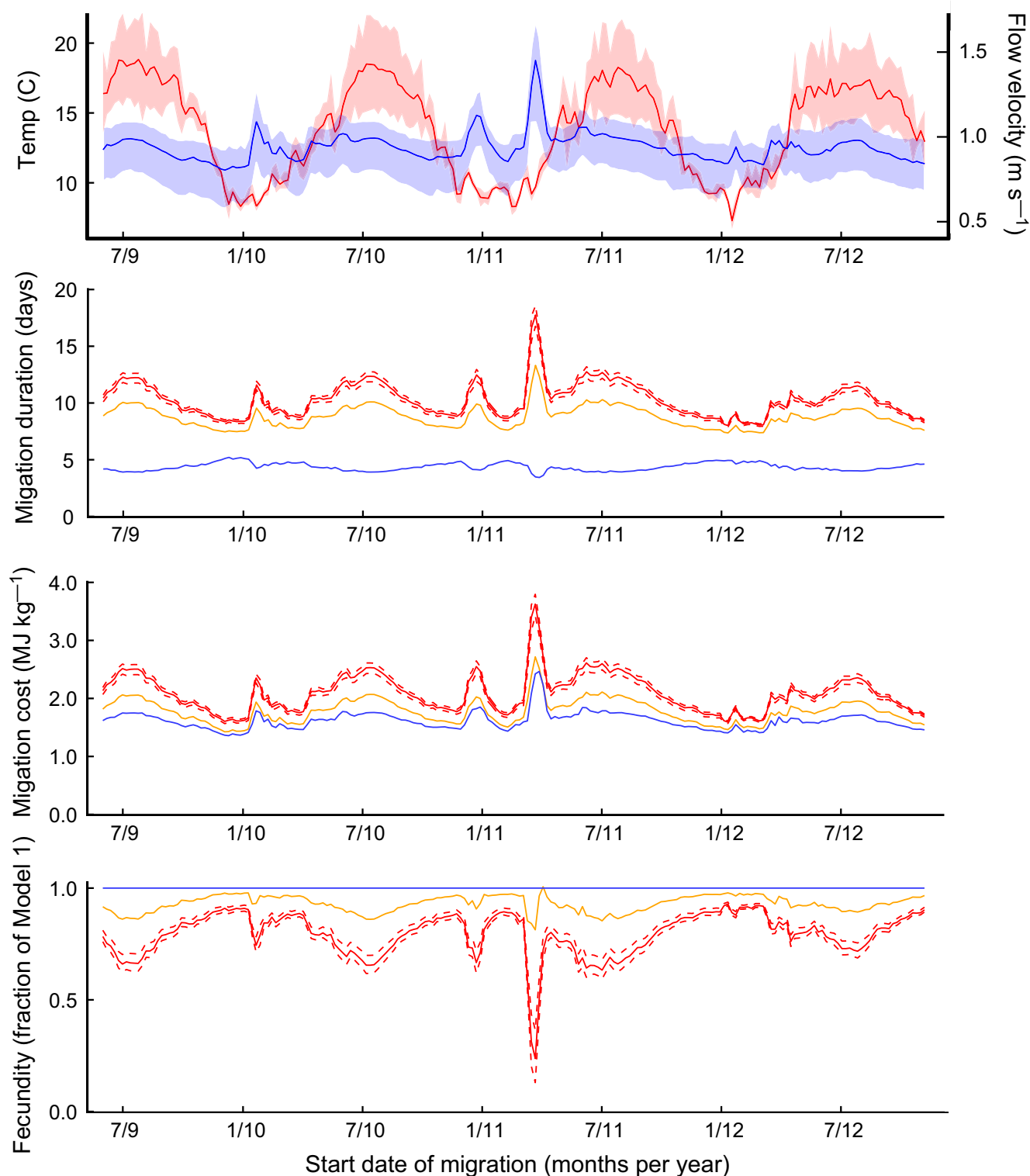
Figure 3 Predictions for migration duration, costs and reproductive investment for a 5 kg Chinook in the Sacramento River as a function of the start date of the migration from models without power constraints (Model 1; blue line), with power constraints (Model 2; orange line), and with power constraints and overhead costs of anaerobic fuel recovery (Model 3; red solid line, dashed lines assume overhead costs of anaerobic fuel recovery ± 25% of our estimated value). The top panel shows the average flow velocity (blue) and temperature experienced by the fish for the range of migration start dates. The shaded areas indicate the interquartile range for temperatures and flow encountered in the simulated salmon runs.
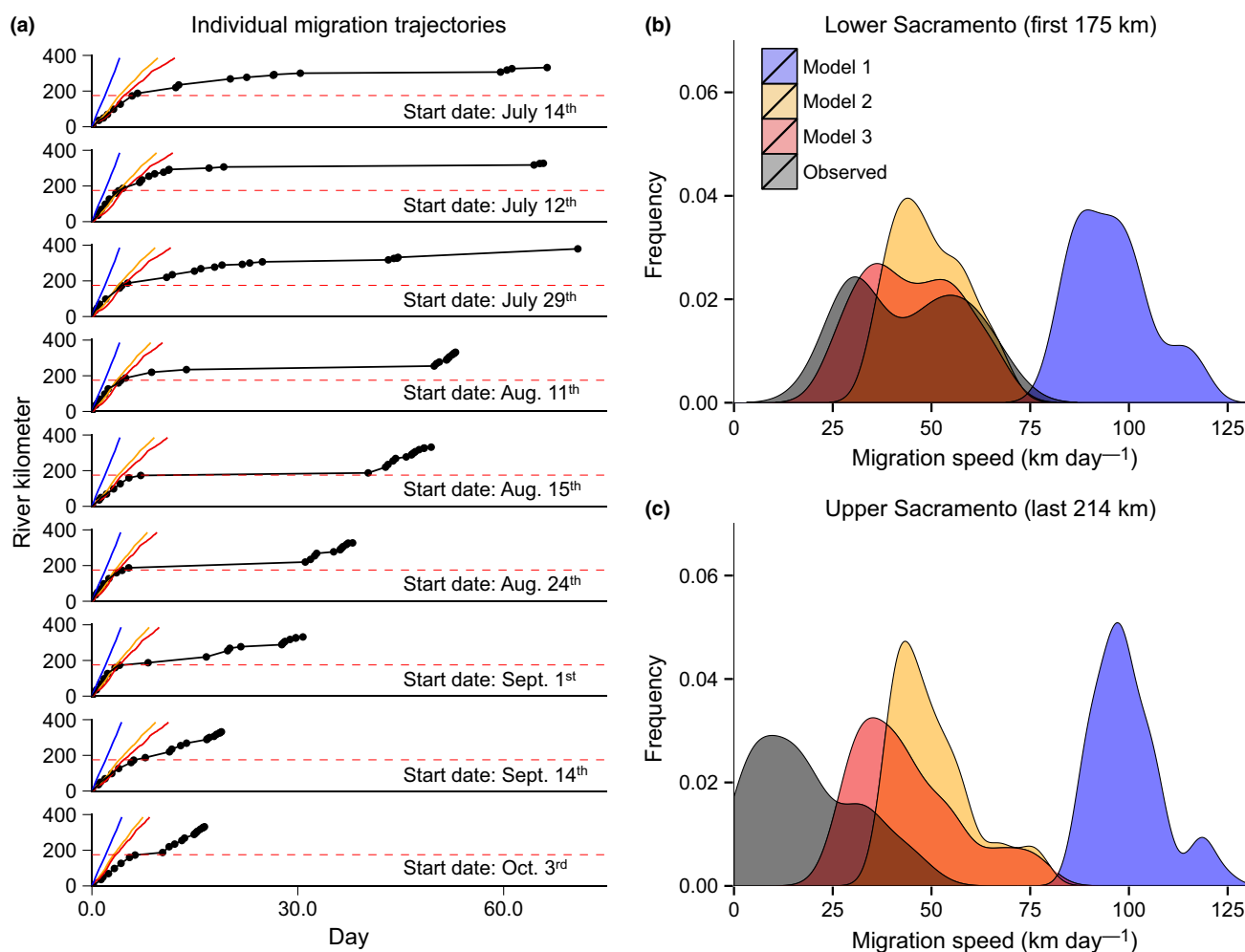
Figure 4 Comparison of observed and predicted migration speeds of the three models. (a) the observed and predicted migration speeds for each of the nine salmon. (b and c) the distribution of observed and predicted migration speeds between monitor locations in the lower 175 km (deep, homogenous and highly leveed) and upper 215 km (un-leveed, heterogeneous, run-riffle river) sections of the Sacramento River.

this period, models incorporating power-constraints and overhead costs of anaerobic recovery result in migratory costs 20–50% greater than those excluding them (Fig. 3).

Whether increased migration costs will result in salmon depleting their energy reserves before reaching the spawning grounds and dying en route, or reaching their spawning grounds with less energy available for allocation to reproduction depends in part on the degree to which gonad maturation occurs during or after the migration. We did not explicitly consider mortality or the timing of allocation to reproduction, so whether costly migrations will result in mortality or reduced fecundity is beyond the scope of this manuscript. Available data suggest that harsh river conditions can result in both increased mortality en route (Rand *et al.* 2006; Farrell *et al.* 2008) and reduced energy investment to reproduction (Kinnison *et al.* 2001). For Pacific salmon, the effects of energetically expensive migrations on reproduction are manifested through reductions in egg size rather than number; Kinnison *et al.* (2001) experimentally manipulated migration difficulty (distance and elevation climb) and found that females with more challenging migrations produced smaller eggs. In turn, egg size is positively correlated with larval size, growth and

survival through the freshwater stage (Beacham *et al.* 1985; Heath *et al.* 1999). Ultimately, size at ocean-entry can strongly affect survival in the first year at sea (Zabel & Achord 2004), especially in years of poor recruitment (Woodson *et al.* 2013).

One novel prediction of the models (2 and 3) incorporating power constraints is that, depending on the flow velocity, the effect of temperature may have either a positive or negative effect on migration speed, consistent with field studies of salmon migratory rates, where positive (Quinn *et al.* 1997; Hasler *et al.* 2012), negative (Goniea *et al.* 2006) and hump-shaped (Salinger & Anderson 2006) temperature effects have been identified. Moreover, our models suggest the relative importance of flow and temperature on migration speed will be context-dependent. In rivers with low flow velocities, migration speed was primarily temperature-dependent and independent of flow velocity (Fig. 2). However, at high velocities, flow velocity surpassed temperature as the primary driver of migration rate. This context-dependent pattern (temperature-dependent migration speeds at low flow velocities and flow-dependent rates at high flow velocities) was the same pattern recently demonstrated in a multi-year, multi-run teleme-

Table 2 Comparison of predicted and observed physiological traits of closely related species

Trait	Prediction	Observation	Units	Species	Source
Anaerobic work capacity	103	115.1–182.2	mgO$_2$ kg^{-1}	Rainbow trout	See refs within Table S3
Recovery time	26.5–45.1*	< 45†	Minutes	Rainbow trout	Jain & Farrell (2003)
		35–45‡		Sockeye and coho	Lee *et al.* (2003)
Excess post exercise oxygen consumption	187.5	62–254	mgO$_2$ kg^{-1}	Sockeye and coho	Lee *et al.* (2003)

Shown are the predicted values for Chinook salmon from the model incorporating power constraints and overhead costs of recovery (Model 3).
*Predicted recovery time depends on fish size and temperature. Shown is the range of recovery times predicted for fish ranging in size from 1 to 10 kg and temperatures ranging from 10 to 20 °C.
†Estimated from time needed for equivalent swim performance in repeated 'critical swim speed' tests.
‡Estimated from time to return to within 20% of resting VO$_2$.

try study of Klamath River Chinook (see fig. 6 in Strange 2012).

In the Sacramento River, models including power constraints had improved capacity to predict observed migration speeds. This was especially true for the lower, highly channelised river section (Fig. 4b). For the upper section, the models including power constraints still performed better, but they nevertheless overestimate observed migration speeds of Chinook. One potential explanation is that the 1-dimensional representation of the river hydraulics does not capture the heterogeneous velocity field in the upper Sacramento River. One promising area for future development is to evaluate how constraints on power influence the least cost path of migration in heterogeneous velocity fields (McElroy *et al.* 2012). Alternatively, the migration speed of salmon may be determined by factors other than the minimisation of instantaneous *COT* such as minimising total migration costs. For example, fish that initiate their spawning migration early may migrate more slowly as they will still have to pay maintenance costs at the spawning grounds while they wait for the optimal spawning time. This hypothesis is supported by the strong propensity for early arriving Chinook to hold for long periods of time between telemetry monitor locations in the upper Sacramento River (Fig. 4a).

We made several simplifying assumptions about the physiological mechanisms underpinning exhaustion and recovery. Nevertheless, the model predictions correspond closely with observations of anaerobic work capacity, recovery times and excess post-exercise oxygen consumption of closely related species (summarised in Table 2). Furthermore, our model predicts the commonly observed behaviour that fish swim at steady speeds at low flow velocities and switch to a burst-recovery strategy at high flow velocities (Ellis 1966; Hinch *et al.* 2002; Makiguchi *et al.* 2008).

Concepts from sports science were useful for predicting the consequences of metabolic power constraints for migrating salmon because salmon share a critical feature with human athletes: they engage in metabolically demanding activities that are constrained by power supply. Salmon are not unique in this respect, thus the concepts we developed will be applicable to a broad range of species and contexts. One general application of our work is quantifying the cost of rising temperatures on ectothermic animals. Our framework allows for calculating the costs of rising temperatures (in terms of both lost time and energy needed to recover anaerobic fuels) for species that engage in behaviours with power demands exceeding their critical power. For feeding animals, the loss of time has an additional opportunity cost, in that time spent recovering anaerobic fuels cannot be spent foraging.

AUTHORSHIP

BTM developed the initial concept for the manuscript, implemented the models and wrote the first draft of the manuscript. RMN and EMD contributed to theory development, AP produced the hydraulic model output and CJM produced the telemetry data. All authors contributed substantially to analysis and writing revisions.

REFERENCES

Atkinson, D.E. (1977). *Cellular Energy Metabolism and its Regulation.* Academic Press Inc., London.

Beacham, T., Withler, F. & Morley, R. (1985). Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.*, 63, 847–850.

Bender, D.A. (2012). The metabolism of "surplus" amino acids. *Br. J. Nutr.*, 108(Suppl), S113–S121.

Bernatchez, L. & Dodson, J. (1985). Influence of temperature and current speed on the swimming capacity of lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*). *Can. J. Fish Aquat. Sci.*, 42, 1522–1529.

Billat, V., Hamard, L., Koralsztein, J.P. & Morton, R.H. (2009). Differential modeling of anaerobic and aerobic metabolism in the 800-m and 1,500-m run. *J. Appl. Physiol.*, 107, 478–487.

Clarke, A. & Pörtner, H.O. (2010). Temperature, metabolic power and the evolution of endothermy. *Biol. Rev. Camb. Philos. Soc.*, 85, 703–727.

Crossin, G., Hinch, S., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J. et al. (2004). Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *J. Fish Biol.*, 65, 788–810.

Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M. et al. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science*, 332, 109–112.

Ellis, D. (1966). Swimming speeds of sockeye and coho salmon on spawning migration. *J. Fish. Board Can.*, 23, 181–187.

Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M. et al. (2008). Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiol. Biochem. Zool.*, 81, 697–708.

Garland, T. (1984). Physiological correlates of locomotory in a lizard : an allometric approach performance. *Am. J. Physiol.*, 247, 806–815.

Geist, D.R., Brown, R.S., Cullinan, V.I., Mesa, M.G., VanderKooi, S.P. & McKinstry, C.A. (2003). Relationships between metabolic rate, muscle electromyograms and swim performance of adult chinook salmon. *J. Fish Biol.*, 63, 970–989.

Gleeson, T.T. (1996). Post-exercise lactate metabolism: a comparative review of sites, pathways, and regulation. *Annu. Rev. Physiol.*, 58, 565–581.

Goniea, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H. & Stuehrenberg, L.C. (2006). Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. *Trans. Am. Fish. Soc.*, 135, 408–419.

Hancock, T.V. & Gleeson, T.T. (2008). Contributions to elevated metabolism during recovery: dissecting the excess postexercise oxygen consumption (EPOC) in the desert iguana (*Dipsosaurus dorsalis*). *Physiol. Biochem. Zool.*, 81, 1–13.

Hasler, C., Mossop, B., Patterson, D., Hinch, S. & Cooke, S. (2012). Swimming activity of migrating Chinook salmon in a regulated river. *Aquat. Biol.*, 17, 47–56.

Heath, D., Fox, C. & Heath, J. (1999). Maternal effects on offspring size : variation through early development of Chinook salmon. *Evolution*, 53, 1605–1611.

Hein, A.M. & Keirsted, K.J. (2011). The rising cost of warming waters: effects of temperature on the cost of swimming in fishes. *Biol. Lett.*, 8, 266–269.

Hinch, S., Standen, E., Healey, M. & Farrell, A. (2002). Swimming patterns and behaviour of upriver-migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada. *Aquat. Telem.*, 165, 147–160.

Jain, K.E. & Farrell, A.P. (2003). Influence of seasonal temperature on the repeat swimming performance of rainbow trout *Oncorhynchus mykiss*. *J. Exp. Biol.*, 206, 3569–3579.

Jones, A.M., Vanhatalo, A., Burnley, M., Morton, R.H. & Poole, D.C. (2010). Critical power: implications for determination of V̇O2max and exercise tolerance. *Med. Sci. Sports Exerc.*, 42, 1876–1890.

Kinnison, M.T., Unwin, M.J., Hendry, A.P. & Quinn, T.P. (2001). Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution*, 55, 1656–1667.

Lee, C.G., Farrell, A.P., Lotto, A., Hinch, S.G. & Healey, M.C. (2003). Excess post-exercise oxygen consumption in adult sockeye (Oncorhynchus nerka) and coho (O. kisutch) salmon following critical speed swimming. *J. Exp. Biol.*, 206, 3253–3260.

Liao, J.C. (2007). A review of fish swimming mechanics and behaviour in altered flows. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 362, 1973–1993.

Makiguchi, Y., Nii, H., Nakao, K. & Ueda, H. (2008). Migratory behaviour of adult chum salmon, *Oncorhynchus keta*, in a reconstructed reach of the Shibetsu River. *Fish. Manage. Ecol.*, 15, 425–433.

McElroy, B., DeLonay, A. & Jacobson, R. (2012). Optimum swimming pathways of fish spawning migrations in rivers. *Ecology*, 93, 29–34.

Monod, H. & Scherrer, J. (1965). The work capacity of a synergic muscular group. *Ergonomics*, 8, 329–338.

Morton, R.H. (2006). The critical power and related whole-body bioenergetic models. *Eur. J. Appl. Physiol.*, 96, 339–354.

Morton, R.H. & Billat, L.V. (2004). The critical power model for intermittent exercise. *Eur. J. Appl. Physiol.*, 91, 303–307.

Oudman, T., Onrust, J., de Fouw, J., Spaans, B., Piersma, T. & van Gils, J.A. (2014). Digestive capacity and toxicity cause mixed diets in red knots that maximize energy intake rate. *Am. Nat.*, 183, 650–659.

Pike, A., Danner, E., Boughton, D., Melton, F., Nemani, R., Rajagopalan, B. et al. (2013). Forecasting river temperatures in real time using a stochastic dynamics approach. *Water Resour. Res.*, 49, 5168–5182.

Plaut, I. (2001). Critical swimming speed: its ecological relevance. *Comp. Biochem. Physiol., Part A Mol. Integr. Physiol.*, 131, 41–50.

Pörtner, H. (2001). Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, 88, 137–146.

Pörtner, H.O. & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, 315, 95–97.

Quinn, T.P., Hodgson, S. & Peven, C. (1997). Temperature, flow, and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Can. J. Fish Aquat. Sci.*, 54, 1349–1360.

Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S. et al. (2006). Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Trans. Am. Fish. Soc.*, 135, 655–667.

Salinger, D.H. & Anderson, J.J. (2006). Effects of water temperature and flow on adult salmon migration swim speed and delay. *Trans. Am. Fish. Soc.*, 135, 188–199.

Strange, J.S. (2012). Migration strategies of adult Chinook salmon runs in response to diverse environmental conditions in the Klamath River Basin. *Trans. Am. Fish. Soc.*, 141, 1622–1636.

Sundström, D., Carlsson, P. & Tinnsten, M. (2014). Comparing bioenergetic models for the optimisation of pacing strategy in road cycling. *Sports Eng.*, 17, 207–215.

Tiidus, P., Tupling, A. & Houston, M. (2012). Biochemistry Primer for Exercise Science, 4E. Human Kinetics Champaign, IL United States.

Vanhooydonck, B., James, R., Tallis, J., Aerts, P., Tadic, Z., Tolley, K. et al. (2014). Is the whole more than the sum of its parts? Evolutionary trade-offs between burst and sustained locomotion in lacertid lizards. *Proc. Biol. Sci.*, 281, 20122677.

Webb, P. (1998). Swimming. In: *The Physiology of Fishes* (ed. Evans, D.H.). CRC Press, Boca Raton, pp. 3–24.

Williams, J. (2006). Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. *San Francisco Estuary Watershed Sci.*, 4, 110–126.

Woodson, L., Wells, B. & Weber, P. (2013). Size, growth, and origin-dependent mortality of juvenile Chinook salmon, *Oncorhynchus tshawytscha,* during early ocean residence. *Mar. Ecol. Prog. Ser.*, 487, 163–175.

Zabel, R. & Achord, S. (2004). Relating size of juveniles to survival within and among populations of Chinook salmon. *Ecology*, 85, 795–806.

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